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A Novel Approach to Egg and Math: Improved Geometrical Standardization of Any Avian Egg Profile

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Abstract

Developing a geometric formulation of any biological object has a number of justifications and applications. Recently, we developed a universal geometric figure for describing a bird's egg in any of the possible basic shapes: spherical, ellipsoidal, ovoid and pyriform. The formulation proved widely applicable but had a number of drawbacks, including a very obvious “join” between two egg parts. To correct this, we developed “the Main Axiom” of the universal mathematical formula. This essentially involved corresponding the ordinate of the extremum of the function to half the maximum egg breadth (B), and the abscissa to the reciprocal of the parameter w that reflects the shift of the vertical axis to its coincidence with B. This, in turn, helped us develop a new, simplified mathematical model without a non-biological “join”. Experimental verification was performed to confirm the adequacy of the new geometric figure. It accurately described actual avian eggs of various shapes more closely than our previous model. To the best of our knowledge, our new, simplified, equation can be accepted as a standard for any bird egg that exists in nature. As a rather simple equation, it can be applied in broad applications.

Introduction

The mathematical description of any biological object is the cornerstone of a range of academic disciplines. It has broad applicability beyond biology in diverse fields such as engineering, construction, art, and fundamental/applied modeling. The most basic shape, the sphere, occurs in nature in the form of some seeds and the eggs of certain birds such as owls. As such, the geometric description of a sphere is well known ($x^2 + y^2 + z^2 = r^2$ where r is the radius) and widely applied. With shapes that are regular along one axis (spheres and all birds eggs are examples) a three-dimensional structure can be projected onto a two-dimensional graph. Thus, describing a sphere simplifies to that of $x^2 + y^2 = r^2$ (the formula of a circle) then, when expressing as plottable graph, transforms as a universally applicable:

$$y = \pm\sqrt{x^2 - r^2}$$

A cartesian form of the equation unlike the parametric version (when x = rcosθ, y = rsinθ) is more attractive to non-mathematicians because of its simplicity and ease of applicability. Similarly, an ellipsoid (3D) object such as an emu's egg can be expressed as a 2D ellipse and the common formula applied:

$$\frac{x^2}{a^2} + \frac{y^2}{b^2} = 1,$$

where a and b are the shortest and longest diameters. This transforms as:

$$y = \pm b\sqrt{1 - \frac{x^2}{a^2}}$$

Despite the inclusion of the ± function (which is absent in parametric equations) this is an equation that is easily applied.

The mathematical formulation describing the contours of the majority of birds' eggs has, for many decades, been led through the development and application of Hügelschäffer's model. As the vast majority of global egg biomass is that of domestic fowl (chicken, duck, goose, quail etc.) and most other birds' eggs are similarly ovoid (literally "egg shaped") then Hügelschäffer's model largely serves as the basis for their description.[1–4] In its most simplistic form Hügelschäffer's model is expressed as:

$$y = \pm\frac{B}{2}\sqrt{\frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2}},$$

where B is the egg maximum breadth, L is the egg length, and w is the parameter that shows the distance between two vertical lines corresponding to the maximum breadth and the half length of the egg, $L/2$.

In order to be truly universal however, the formulation needs to extend to pyriform (cone/pear shaped) eggs such as those laid by guillemots, razorbills, penguins and gulls; Hügelschäffer's model does not adequately describe these. Recently, we[5] reported results involving the development of a universal formula for describing the contours of any bird's egg, including pyriform ones. Moreover, we reported that each of the first three geometric figures can be easily converted into each other by introducing or excluding one of the key parameters, i.e., *B*, *L* or *w*, a process we described, for convenience, as "mathematical evolution" or "mathematical progression".[6] Our breakthrough publication[5] introduced mathematical evolution/progression to pyriform eggs through the equation:

$$y=\pm\frac{B}{2}\sqrt{\frac{L^2-4x^2}{L^2+8wx+4w^2}}\cdot\left(1-\frac{\sqrt{5.5L^2+11Lw+4w^2}\cdot(\sqrt{3}BL-2D_{L/4}\sqrt{L^2+2wL+4w^2})}{\sqrt{3}BL(\sqrt{5.5L^2+11Lw+4w^2}-2\sqrt{L^2+2wL+4w^2})}\cdot\left(1-\sqrt{\frac{L(L^2+8wx+4w^2)}{2(L-2w)x^2+(L^2+8Lw-4w^2)x+2Lw^2+L^2w+L^3}}\right)\right)$$

This caused considerable lay public and scientific interest. The article was widely circulated in international scientific bulletins and online media, including National Geographic España, BBC News Mundo, Science and Vie, Science Bulletin Kent, Sci-News, Yale Scientific, Sciences et Avenir, The Boar, Daily Mail, Frankfurter Allgemeine Sonntagszeitung,[7–16] etc., as well as authored interviews on scientific forums.[11,17–19] In addition, this theoretical finding served as an impetus for its implementation in diverse studies and disciplines. These have embraced (i) a comparative analysis of the "universal formula" with others developed before or after its publication;[20–28] (ii) its use for deriving applied calculation formulae, e.g., for computing egg volume or surface area that can be successfully used in biological, zootechnical and/or other studies;[29–32] (iii) technology developments;[33,34] (iv) space research, e.g., for building egg-shaped lunar habitat structures[35] and modelling broad-line regions when studying supermassive black holes;[36] (v) computer games;[37] and even (vi) interest in its inclusion in the school curriculum in mathematics as an adapted version of our research.[38]

Such unexpected, but welcome, popularity encouraged us to evaluate more seriously the universal formula and its ramifications. Closer examination showed that, despite a close conformation of the extremum to *B*/2, it fluctuated within ±2%. In other words, where the blunt and pointed ends meet, there were clear issues resolving the "join" in the two formulations of each (both individually derived by adapting Hügelschäffer's model). This is depicted in Fig. 1.

It might be argued that this problem is not too important for practical purposes; however, it does not allow us to conclude that a certain clear geometric figure is created, akin, for example, to a sphere or an ellipsoid, that corresponds to any and every egg contour.

A second problem was that the universal formula as depicted above turned out to be too cumbersome and difficult to apply, and this shortcoming was pointed out by a number of authors, ourselves included.[18,25,26,39] In view of this, the purpose of this study was to revise and improve our approach to the development of a more simplified universal formula. To achieve this, we formulated a rule called the "Main Axiom of the Mathematical Formula of the Bird's Egg" (hereafter the "Main Axiom"). This axiom, in essence, lies in the fact that the extremum of the function that describes the egg contour geometry should conform to the value of *B*/2, i.e., half the maximum diameter of the egg. To determine the extremum point, one should find the derivative of the function and equate it to zero. Herewith, the solution should imply the equality of the argument to the value of −*w*, which, along with the aforementioned measures *B* and *L*, is one of the fundamental parameters of the universal formula and means a shift of the vertical axis until it coincides with the maximum diameter (Fig. 1). The theory behind this formulation is given below.

Theory

Theoretical aspects of how to stitch two halves of an egg together

Despite a detailed study of the geometric properties of the Hügelschäffer's model,[40–42] some of its properties have remained under-explored. For instance, if the parameter *w* is growing, then, when it reaches a value equal to half the egg length, *L*/2, the closed ovoid turns into a parabola.[40] Since the hypothesis of constructing a pyriform ovoid in our previous work[5] was grounded precisely on the geometric combination of a classical ovoid and a parabola, we tested the possibility of combining two contours built using Hügelschäffer's model (Fig. 1). Therewith, the ovoid (shown in blue) corresponds to the classical ovoid with parameters *B*, *L* and *w*. For the second figure (depicted in pink), the axis shift, denoted for this contour as w_p, is equal to *L*/2.

Then, if we remove the extra areas highlighted in yellow in Fig. 1, the contours of a classic pyriform ovoid are observed (Fig. 2). Even by visual inspection, however, the “join” is still obvious and clearly not observed in nature.

In order to reconcile the two parts so that the overall profile is more biologically plausible and applicable, particularly at the “join”, we need to take into account how the two were derived using Hügelschäffer's model. We[41] previously adapted the parameters of the bird's egg to describe the blunt end of the egg according to the following mathematical expression:

$$y_b = \pm \frac{B}{2} \cdot \sqrt{\frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2}}\ , \qquad (1)$$

where, as previously stated, *B* is the egg maximum breadth, *L* is the egg length, and *w* is the parameter that reflects the distance between two vertical lines conforming to the maximum breadth and the half length of the egg. Formula (1) corresponds to *x* values within the interval [−*L*/2 ... −*w*].

At the same time, the pointed end, characterized by the interval *x* = [−*w* ... *L*/2], corresponds to the following function:

$$y_p = \pm \frac{B_p}{2} \cdot \sqrt{\frac{L^2 - 4x^2}{L^2 + 8w_p x + 4w_p^2}} \qquad (2)$$

For Eqn2, the values of B_p and w_p do not match those of *B* and *w* in Eqn1 (Fig. 1). While the parameters of Eqn1 can be relatively easily measured either directly on the investigated egg or on its image, the values of B_p and w_p should be calculated.

To establish a probable relationship between B_p and B, we can use the condition that at the point $x = -w$ where both contours coincide, with the value of the function y_p being, according to the principle of the Main Axiom, equal to $y_p = y_b = B/2$. Substituting these data into Eqns1 and 2 and equating them, we get the following equation:

$$B_p = B \cdot \sqrt{\frac{L^2 - 8w_p w + 4w_p^2}{L^2 - 4w^2}} \tag{3}$$

Calculation of the value of w_p is possible only by measuring an additional parameter of the egg. Based on an earlier study,[41] Narushin et al.[5] chose the diameter that is denoted in Fig. 2 as D_p, conforming to the point $x = L/4$ and representing the most informative characteristic of the pointed end of the bird's egg. Measuring the D_p value will enable calculating w_p. To do this, we substitute the value $x = L/4$ into Eqn2. Considering Eqn3 and the fact that at this point (i.e., $x = L/4$), the value $y_p = D_p/2$, we obtained the desired formula for such a recalculation as follows:

$$w_p = L\left(\frac{\left(\frac{D_p}{B}\right)^2\left(1-4\left(\frac{w}{L}\right)^2\right)+3\frac{w}{L}}{3-4\left(\frac{D_p}{B}\right)^2\left(1-4\left(\frac{w}{L}\right)^2\right)} - \sqrt{\left(\frac{\left(\frac{D_p}{B}\right)^2\left(1-4\left(\frac{w}{L}\right)^2\right)+3\frac{w}{L}}{3-4\left(\frac{D_p}{B}\right)^2\left(1-4\left(\frac{w}{L}\right)^2\right)}\right)^2 - \frac{1}{4}}\right) \tag{4}$$

A detailed output of Eqn4 and verification of its correctness are given in Supplementary Material S1.

The above preparatory work was thus successfully completed, and, as a result, it remained to develop a mechanism “stitching” mathematically two halves of the egg, with one conforming to the blunt end in the interval $x = [-L/2 \ldots -w]$ (Eqn1) and the other conforming to the pointed end in the interval $x = [-w \ldots L/2]$ (Eqn2). An aggregate of these functions (Eqns1 and 2) is piecewise functions,[43] and one can unite this aggregate into one equation only under a numerical procedure. Orszulik[44–46] proposed an elegant and logical approach to such a combination of two functions. Following this method, one of the equations is taken as the main one, to which the functional difference of the combined equations is mathematically added, being multiplied by a certain joining function. The proposed procedure logic is fully suited to the goal of stitching our egg halves. If we choose y_b (Eqn1) as the base function, the difference $(y_b - y_p)$ will characterize the yellow zones in Fig. 1, which we need to remove. For this purpose, we will introduce some kind of joining function, y_j. Denoting the generalized function of the combined egg profile as y, we can write this relationship mathematically as follows:

$$y = y_b + (y_p - y_b)y_j \tag{5}$$

According to Orszulik,[46] the joining function y_j varies from 0 to 1 and is most easily expressed by the classical sigmoid equation. However, as it turned out in the course of further mathematical transformations, the sigmoid has a number of disadvantages when used to connect the two halves of the egg into a single harmonious circuit. This concerned the limited interval validity of the exponent that is part of the sigmoid, as well as the transformation of its derivative under certain conditions to infinity, which prevented the compliance with the Main Axiom conditions. As a result, we chose the joining function as an algebraic one, being related to so called S-curves.[47] Considering that, in our case, the inflection point of the selected S-curve should be located on the vertical axis $x = -w$ (Fig. 1), since it is at this point that one egg profile is replaced by another, we can write the joining function formula in the following general form:

$$y_j = a_j + b_j \frac{x+w}{\sqrt{c_j + (x+w)^2}}, \qquad (6)$$

in which a_j, b_j and c_j are coefficients.

To determine the coefficients in Eqn6, we used the following assumptions: (i) when $x = -L/2$, $y_j = 0$; (ii) when $x = L/2$, $y_j = 1$; and (iii) when $x = -w$, $y_j = ½$. This allowed us to deduce the final formula of the joining function as follows:

$$y_j = \frac{1}{2}\left(1 + \frac{x+w}{\sqrt{(x+w)^2}}\right) \qquad (7)$$

A detailed derivation and analysis of Eqn7 are presented in Supplementary Material S2. Then, taking into account Eqns 1–3 and 7, the final form of the mathematical function that describes the contours of the egg (i.e., Eqn5) will be as follows:

$$y = \pm\frac{B}{2}\left[\sqrt{\frac{L^2-4x^2}{L^2+8wx+4w^2}} + \frac{1}{2}\left(\sqrt{\frac{(L^2-4x^2)(L^2-8w_p w+4w_p^2)}{(L^2+8w_p x+4w_p^2)(L^2-4w^2)}} - \sqrt{\frac{L^2-4x^2}{L^2+8wx+4w^2}}\right)\left(1+\frac{x+w}{\sqrt{(x+w)^2}}\right)\right] \qquad (8)$$

To validate the above mathematical expression, it is necessary to make sure that it conforms to the two postulates formulated in the Introduction section, i.e., (i) the fulfilment of the Main Axiom and (ii) the equality $y = B/2$ when $x = -w$. The latter is easy enough to confirm after the appropriate substitution of $x = -w$ in Eqn8. On the other hand, to confirm the Main Axiom, one needs to differentiate Eqn8, and then equate it to zero. If this equality is approved at the value $x = -w$, it can be argued that the resulting Eqn8 is adequate and valid. Since the resulting function (Eqn8) is rather complicated for finding the derivative, we will take as a basis the original Eqn5 and proceeded with the differentiation as follows:

$$\frac{\partial y}{\partial x}=\frac{\partial y_b}{\partial x}+\left(\frac{\partial y_p}{\partial x}-\frac{\partial y_b}{\partial x}\right)y_j+(y_p-y_b)\frac{\partial y_j}{\partial x} \qquad (9)$$

The solution of Eqn9 was reduced to inferring the derivatives of the component functions, y_b (Eqn1), y_p (Eqn2) and y_j (Eqn7). After making the respective mathematical transformations and substitution of the value $x = -w$ into the resulting equation, the conformation of Eqn8 to the Main Axiom was validated. That is, the extremum of the resulting function y is at the point $-w$ on the horizontal axis. A detailed description of producing the derivatives and further mathematical transformations of the function y (Eqn8) can be seen in Supplementary Material S3.

The fulfilment of all the conditions for the mathematical adequacy of the resulting model does not necessarily mean that it is biologically applicable. In other words, the question of its match with profiles of actual eggs remains. Because pyriform eggs cause the greatest complexity in their mathematical description, it was precisely such a contour that was chosen to evaluate the similarity (match) criterion. In this respect, the extreme pyriform profile was chosen, when the value $w_p = L/2$, and the pointed end of the egg conforms to a parabola.[40] The results of this match test are shown in Fig. 3.

The resulting egg profile still has a clear and obvious join at the point $x = -w$ and, because of that, cannot meet the similarity criterion, since such eggs clearly do not exist in nature. Thus, the objective of the current study was dedicated to not only to piecing together its two halves, but also to further removal (“smoothing”) of this non-biological interface.

We assumed that, based on the principles of synergy, the number of options for combining profiles should also radically affect the quality characteristics of the resulting function. In other words, it is worth undertaking one more attempt to merge the egg profiles using, as a formula for the pointed end of the egg, the combination we have already obtained, i.e., function y in Eqn8, instead of Eqn2. Denoting the new resulting function as Y, and, accordingly, the new joining function as Y_j, by analogy with Eqn5, we can use:

$$Y = y_b + (y - y_b)Y_j \qquad (10)$$

If we substitute the value of y from Eqn5 into Eqn10, we get a more convenient formula for the Y function:

$$Y = y_b + (y_p - y_b)y_jY_j \qquad (11)$$

Thus, if the contour smoothing procedure can be carried out in this way, then, the synergy will conform to the product of the joining functions y_j and Y_j.

Before selecting the joining function Y_j, we decided to check how much its algebraic formula will affect the compliance with the Main Axiom, i.e., the location of the extremum of the function Y (Eqn11), for which the corresponding differentiation was carried out. A detailed process of differentiating the function Y (Eqn11) and verifying if the extremum of the function meets the conditions of the Main Axiom is shown in Supplementary Material S4.

The results of differentiation were most satisfactory. The form of the joining function Y_j had no effect on the location of the extremum, which always appeared in the predicted place, i.e., conform to match $x = -w$. Inspired by the conformity of synergy process and being mindful of the goal to make the final formula as simple as possible, we decided to take the linear function as the basis for Y_j that would be the most simple and suitable in subsequent calculations:

$$Y_j = A_j x + B_j \,, \tag{12}$$

where A_j and B_j are coefficients to be determined.

To determine the coefficients of equation (12), we used the following reasoning and assumptions.

When analyzing the resulting egg profile after the first stage of combining the two halves, it looks obvious that smoothing will not reduce the diameter of the pointed end sharply, but gradually, presumably, in the interval from $x = 0$ to $x = L/4$. The latter point is one of the most informative egg variables,[5] being also used in this study for the recalculation of w_p (Eqn4), therefore, its value should remain unchanged. Then, at $x = 0$, the respective function value $Y(0)$ should prevail the analogous meaning of $y_p(0)$ being just between two functions, $y_b(0)$ and $y_p(0)$ (as explained in Fig. 4) and recalculated as follows:

$$Y(0) = y_p(0) + K\left(y_b(0) - y_p(0)\right), \tag{13}$$

where K is a smoothing coefficient, varying from 0 to 1.

Accordingly, at the point $x = L/4$, the value of the function $Y(L/4)$ should be equal to the analogous meaning of $y_p(L/4)$. These prerequisites allowed us to obtain the final formula of the joining function Y_j:

$$Y_j = \frac{2}{L}x + \frac{1}{2} \tag{14}$$

A detailed derivation and analysis of Eqn14 are presented in Supplementary Material S5. Thus, the resulting function Y (Eqn11) can be written as follows:

$$Y = \pm\frac{B}{2}\left[\sqrt{\frac{L^2-4x^2}{L^2+8wx+4w^2}} + \frac{4x+L}{4L}\left(\sqrt{\frac{(L^2-4x^2)(L^2-8w_p w+4w_p^2)}{(L^2+8w_p x+4w_p^2)(L^2-4w^2)}} - \sqrt{\frac{L^2-4x^2}{L^2+8wx+4w^2}}\right)\left(1+\frac{x+w}{\sqrt{(x+w)^2}}\right)\right] \tag{15}$$

Using the same extreme pyriform variant (w_p = L/2) as before (Fig. 3), we tested the obtained function (Eqn15), the results of which are shown in Fig. 4.

The resulting contour (Fig. 4) fully complies with the principles of both the Main Axiom and similarity, and it could be argued therefore that the theoretical investigation was successfully carried out, if not for two more aspects that we needed to clarify: First, this is the form of the resulting joining function, which is the synergistic product of y_j and Y_j. Based on Eqn11:

$$y_j Y_j = \left(1+\frac{x+w}{\sqrt{(x+w)^2}}\right)\cdot\frac{4x+L}{4L} \tag{16}$$

The visual interpretation of Eqn16 is provided in Fig. 5.

The appearance of the resulting connecting function turned out to be logical. However, it was impossible to predict it in advance at the first stage of combining two egg halves. As a result of which, we aimed to provide the second aspect, namely, to increase the simplicity and convenience of the developed egg profile formula to facilitate the efficient application of any scientific development. In this regard, we slightly transformed the components of Eqn11 whereupon it acquired the following form:

$$Y=\pm\frac{B}{2}\left[\frac{1}{\sqrt{1+4\dfrac{(x+w)^2}{L^2-4x^2}}}+\left(\sqrt{\frac{1+4\dfrac{(w-w_p)^2}{L^2-4w^2}}{1+4\dfrac{(x+w_p)^2}{L^2-4x^2}}}-\frac{1}{\sqrt{1+4\dfrac{(x+w)^2}{L^2-4x^2}}}\right)\left(1+\frac{x+w}{\sqrt{(x+w)^2}}\right)\left(\frac{x}{L}+\frac{1}{4}\right)\right] \tag{17}$$

The variable w_p in Eqn17 is calculated according to Eqn4. The resulting formula (17) is quite compact and suitable for subsequent programming and/or mathematical transformations since it does not contain polynomials. It is also simpler than our previous calculations and, mindful of the fact that the elements (x + w) and ($L^2 - 4x^2$) are repeated a few times, we can replace these and others with letters thus:

$C = x + w$
$D = L^2 - 4x^2$
$E = w - w_p$
$F = x + w_p$

Then the simplified formula becomes:

$$Y=\pm\frac{B}{2}\left[\frac{1}{\sqrt{1+4\dfrac{C^2}{D}}}+\left(\sqrt{\frac{1+4\dfrac{E^2}{D}}{1+4\dfrac{F^2}{D}}}-\frac{1}{\sqrt{1+4\dfrac{C^2}{D}}}\right)\left(1+\frac{C}{\sqrt{C^2}}\right)\left(\frac{x}{L}+\frac{1}{4}\right)\right] \tag{18}$$

A similar simplification can be undertaken with Eqn4 if to make the following replacement:

$$A=\frac{\left(\frac{D_p}{B}\right)^2\left(1-4\left(\frac{w}{L}\right)^2\right)+3\frac{w}{L}}{3-4\left(\frac{D_p}{B}\right)^2\left(1-4\left(\frac{w}{L}\right)^2\right)}$$

Then

$$w_p=L\left(A-\sqrt{A^2-\frac{1}{4}}\right) \tag{19}$$

The formula can thus be derived from four unknowns, L, B, w, and w_p. The first three are direct egg measurements, the last needs to be calculated using D_p, which is the diameter at $L/4$. Therefore, when we use four measurements from the egg, L, B, w, and D_p, we can mathematically describe any egg shape.

Biological aspects of what a standard egg looks like

The question of the existence of a certain standard for a bird's egg has occupied the minds of poultry scientists for decades. Indeed, by obtaining standard eggs as a result of breeding programs, it is possible to increase hatchability significantly, simplify the procedure for sorting eggs, unify packaging and equipment for technological maintenance, and optimize the egg storage process.[48–53]

Perhaps the first to propose the parameters of a standard chicken egg were Romanoff and Romanoff.[54] They determined a number of geometric measurements that are still considered the classic geometric interpretation of the ideal egg-shaped ovoid, under the contours of which most poultry eggs fall. Here, we explored how successfully this standard can be reproduced by the universal model of the bird's egg, i.e., Eqn17 we have derived. The data presented by Romanoff and Romanoff,[54] as well as the image of the egg profile itself, allowed us to calculate and/or measure the missing parameters, in particular w and D_p, and reproduce both profiles using MS Excel (Fig. 6). When reproducing the contour of the standard egg of Romanoff and Romanoff,[54] we also depicted the main criteria they presented in their image and in addition to the dimensions they indicated: dividing the segment into three equal parts and the angle of inclination of a certain area.

The visualization of both profiles of the same egg in Fig. 6 showed an almost perfect match. Thus, we obtained similar results when applying different approaches to the search for a definite "egg" standard, i.e., (i) empirical, based on numerous measurements of many eggs, and (ii) theoretical, based on the development of a mathematical model of a certain geometric figure, the profile of which conforms to the main egg forms.

On the other hand, a number of eggs found in nature cannot boast of their resemblance to the standard counterpart (Fig. 6). However, this does not mean that they do not have their own standard profile, in other words, a virtual double, which they do not match. As an example, we provided an image of a chicken egg one of the authors found in his backyard, along with its standard profile calculated by Eqn17 (Fig. 7). For a better perception of this image, as well as all subsequent ones presented in this work, we unified the length of the eggs under the standard egg size of Romanoff and Romanoff,[54] i.e., L = 5.7 cm, with the proper recalculation of all other measured parameters.

Implementation of the biological and mathematical research outlined above inspired us to formulate the following questions, the answers to which could become prerequisites for possible systematics of oological material in terms of unifying the whole variety of their shapes:

1. How accurately can the theoretical egg contour model (Eqn17 and 18) describe actual bird eggs that fall into different shape types, i.e., spherical, ellipsoidal, classic ovoid, and especially pyriform?
2. To what extent do actual eggs meet their mathematical standard (Eqn17 and 18)?

Methods

Since pyriform eggs were the stumbling block in the mathematical description of egg contours,[28,55] the focus of our research on the possibility of egg shape description using Eqn17 and its compliance with the geometric standard was given to this particular category. Hereby, a pyriform profile meant not a purely visual assessment of the degree of pear-shapedness of their pointed end, but a distinct mathematical calculation.

When deducing the mathematical model of bird egg contours (Eqn17), we proceeded from the fact that the value of the calculated parameter w_p is limited by two key points: (i) $w_p = w$, when the pear-shaped profile turns into a classic egg-shaped ovoid and corresponds to the Hügelschäffer's model (Eqn1); and (ii) $w_p = L/2$ that conforms to the highest degree of pyriform end (Supplementary Material S1):

$$w < w_p \leq \frac{L}{2} \tag{20}$$

Indeed, if we substitute the value $w_p = w$ into Eqn17, then, this universal formula is transformed into the Hügelschäffer's model for classical egg-shaped ovoids (Eqn1). Accordingly, if we use the value $w_p = L/2$ in Eqn17, the equation responsible for describing the pointed end (Eqn2) is converted into a parabola formula that can be used as the extreme degree of pyriform eggs. Thus, Eqn20 is a mathematical criterion for conditionally classifying an egg as a pyriform one.

In the course of our previous studies,[6,28,29,34,41,56] we accumulated a large number of photographic and digital images of various eggs obtained directly by us or available in open sources. Thanks to this, we selected the egg images that can be classified as pyriform from 32 bird species. These were subject to subsequent processing and examination. A detailed listing and description of the sources from which the appropriate images were taken was given in Narushin et al.[56] Digital and photographic images of chicken eggs were also used; their detailed description, along with a method for obtaining them, was laid out in Narushin et al.[41]

Since chicken eggs relate to the category of classical ovoids and, in accordance with our previous studies,[28,41] are described by the respective Hügelschäffer's model for classical ovoids (Eqn1), three characteristic egg shapes were chosen for these experiments: elongated, standard and round. This sample, in our opinion, was sufficient to conclude that the derived egg profile formula (Eqn17) is universal.

One of the goals of this work was to ensure methodically the possibility of similar and/or more narrowly focused studies using the universal Eqn17 without employing any sophisticated equipment or software. In this respect, our measurements of egg parameters *B*, *L*, and *w* values (in pixels), as well as processing the results and building standard profiles (i.e., according to Eqn17) for each investigated egg, were carried out using a broadly available software, such as Microsoft Office Picture Manager and Microsoft Office Excel.

Results

For better visualization of the experimental results, the images of real eggs were placed and fit onto the contours of their appropriate standard profile plotted according to formula (17). The length of every egg under study was adjusted to the size of the standard egg established by Romanoff and Romanoff,[54] with L = 5.7 cm, and all other measured parameters were recalculated in the same manner as shown in Fig. 7.

Since, in order to carry out a comparative analysis of eggs of different species, shapes and sizes, it is much more convenient and efficient to use not the initial sizes, but their certain ratios,[5,29,34] we presented numerical data characterizing each egg in the form of the following ratios: B/L, w/L, and D_p/B. To make it clearer what is the difference between the Hügelschäffer's model used to describe the blunt end, from the Hügelschäffer's model for the pointed end, we also gave the values of the ratio w_p/L after the respective calculation of the value of w_p according to formula (4).

By way of example, Fig. 8 reflects the results for three characteristic pyriform eggs. For a more complete visual comparison of pyriform eggs with their standard profiles, see Supplementary Material S6. To demonstrate the differences between the new (Eqn17) and old[5] versions of the egg profile mathematical model, we presented these both egg contour options in Fig. 8.

For a more convenient perception and possible comparative analysis of the advantages of the new equation over the previous one,[5] we also presented the value of the total error in describing the contours of the eggs shown in Fig. 8 for each of the two formulae. To estimate the degree of correspondence of each theoretical egg profile to the actual one, the approximating mean percentage error, ε,[57] was applied:

$$\varepsilon = \frac{1}{k} \cdot \sum_{1}^{n} \left| \frac{v_1 - v_2}{v_1} \right| \cdot 100\% , \qquad (21)$$

where k is a number of x points on the horizontal axis; and v_1 and v_2 are the relevant values of y produced respectively by (1) direct measurement of the egg profile and (2) computation using the corresponding theoretical model.

When defining the egg contours of *Alca torda* (Fig. 8A), ε = 4.0 and 4.1, respectively for the new (Eqn17) and old[5] models. For the eggs of *Aptenodytes patagonicus* (Fig. 8B), these values were ε = 2.8 and 3.2, and for those of *Leucophaeus (Larus) atricilla* (Fig. 8C), ε = 3.6 and 5.5, accordingly.

Thus, the previous universal formula[5] and the new one (Eqn17) quite accurately described the contours of various egg profiles. A more essential drawback and limiting factor in the formulae application may be the mismatch to the Main Axiom. This can be tested by calculating B and w that shows how much B is shifted from the center of the egg. In particular, the B value for the *Alca torda* egg (Fig. 8A) was 3.21 cm (in conventional sizes used for graphical interpretation of the egg contours). This value absolutely conformed to the true value, while the earlier universal formula[5] resulted in B equal to 3.22 cm, i.e., a somewhat overestimated value. Similarly, the value of the parameter w also differed for the two mathematical profile models. If for Eqn17 it absolutely exactly coincided with the true measurement and was equal to 0.80 cm, use of the old formula[5] led to w = 0.99 cm. Similar disproportions were noted for other eggs. The B and w values corresponded exactly to their true values 4.2 cm and 0.40 cm when describing the *Aptenodytes patagonicus* egg using Eqn17 (Fig. 8B), while these values based on the old formula[5] were 4.3 cm and 0.48 cm, respectively. The same discrepancy was noted for the egg profile of *Leucophaeus (Larus) atricilla* (Fig. 8C). Calculated values using the new formula (Eqn17) were in agreement with the actual measurements (B = 3.8 cm and w = 0.44 cm), but in contrast to the values obtained using the old formula[5] (B = 3.9 cm and w = 0.48 cm, respectively).

The results of a comparative analysis of chicken eggs, as representatives of the classical ovoid form, are given in Fig. 9.

Discussion

A circle can be perfectly described mathematically using just one measurement (the radius). An ellipse has just two measurements. Hügelschäffer's model produces a good egg shape using only three measurements, but this has proved insufficient to model all egg shapes. Our previous work[5] on this topic used the Hügelschäffer's model as the basis for an improved model using one additional measurement, thereby enabling a better fit at the pointy end. Though this last model gave a very good fit for most egg shapes, not all the extremes of the egg shape fitted perfectly.

When modelling data such as an egg shape it is clearly important to achieve a good fit – but it is possibly even more important that the extremities of the data are accurately described since they are the most influential. It is also very desirable that the model should consist of a single, complete equation; there should be no variable to estimate and should preferably not be a pair of parametric equations. In this article we put forward the Main Axiom to capture these objectives and have presented a solution to this axiom using purely mathematical techniques. Thus, Eqn17, together with Eqn4, provide a model that, for the first time, exactly describes the extremities of any avian egg. Previous models[5] have provided a very good fit with the data, but some have not been single, complete, equations, and none have been able to provide an exact fit at the extremities. Accurately modelling the extremities is particularly important for an egg shape because a small change in the fit at the widest point results in a large shift in its position; that is, because the slope is shallow at the widest point, a small variation at this point result in a large change to the value of *w*.

The model presented in this article has been achieved using the novel technique of marrying up two shapes using a joining function, and smoothing the transition between the two shapes without any distortion to the extremes. Such an approach to modelling shapes, or indeed modelling any data, may well find valuable application in many other fields of mathematics and engineering. Furthermore, the type of geometric joining function described in this article is novel and may well inform other researchers when modelling data.

Conclusion

In summary, the model described in this article has a number of advantages as follows. (1) It models the extremities of the egg shape exactly (conforms to the Main Axiom) and is thus visually an improvement on previous models. (2) It is a single equation (not parametric) and not requiring estimation of any variables. (3) It is based purely on mathematics. (4) It is based on just four egg parameters and does not use high degree polynomials – just squares and square roots. (5) It is understandable, in that the equation consists of three parts, two for each shape being joined and one joining function. (6) It is applicable to any avian egg shape (spherical, ellipsoidal, ovoid and pyriform). (7) The novel approach described here may be used by others when modelling complex data.

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Author contributions

Conceptualization, investigation, methodology, software, validation and writing – original draft: V.G.N. and S.T.O. Data curation: S.T.O. Formal analysis: V.G.N. Project administration: M.N.R. Supervision: D.K.G. Visualization, V.G.N., S.T.O. and M.N.R. Writing – review & editing: V.G.N., S.T.O., M.N.R. and D.K.G.

Supporting information

Additional supporting information may be found in the online version of this article.

Supplementary Material S1. Deducing a formula for recalculating of w_p using D_p.

Supplementary Material S2. Derivation of the calculation formula for the joining function, y_j.

Supplementary Material S3. Differentiating the function *y* (Eqn8 in the paper) and finding its extremum.

Supplementary Material S4. Differentiating the function *Y* (Eqn11 in the paper) and finding its extremum.

Supplementary Material S5. Derivation of the calculation formula for the joining function, Y_j.

Supplementary Material S6. Pyriform egg examples.

Competing interests

The authors have no conflict of interest to declare.

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Figure legends

Figure 1. Combination of two Hügelschäffer's models conforming to (i) a classical ovoid with parameters *B*, *L* and *w* (blue line) and (ii) a parabolic ovoid whose axial shift corresponds to half the egg length, i.e., $w_p = L/2$.

Figure 2. Pear-shaped ovoid constructed by combining two Hügelschäffer's models (based on Figure 1 above).

Figure 3. Visual interpretation of *y* (Eqn8) as a combination of the functions y_b (Eqn1) and y_p (Eqn2), when $w_p = L/2$.

Figure 4. Visualization of the comparative analysis of the functions *y* (Eqn8) (blue line) and *Y* (Eqn15) (yellow line).

Figure 5. The visual representation of Eqn16.

Figure 6. A standard (or "ideal") chicken egg according to Romanoff and Romanoff[54] (blue line) in comparison with its mathematical equivalent according to Eqn17 (yellow line).

Figure 7. An abnormally shaped chicken egg in comparison with its mathematical standard profile (blue line) plotted according to Eqn17.

Figure 8. Examples of pyriform eggs as compared to their mathematical standard profiles according to Eqn17 (blue line). The top three eggs conform to the egg profile mathematical model according to Eqn17, and the bottom three eggs to Narushin et al.[5] models. A. *Alca torda* (razorbill; https://www.flickr.com/photos/blackcountrymuseums/5237094139/; Black Country Living Museum; CC-BY-NC-SA 2.0); B. *Aptenodytes patagonicus* (king penguin; https://commons.wikimedia.org/wiki/File:Manchot_royal_MHNT.jpg; Muséum de Toulouse; CC-BY-SA-3.0); C. *Leucophaeus* (*Larus*) *atricilla* (Laughing gull; https://commons.wikimedia.org/wiki/File:Larus_atricilla_MWNH_0343.JPG; Natural History Collections of the Museum Wiesbaden; CC-BY-SA-3.0).

Figure 9. Chicken (*Gallus gallus*) eggs in comparison with their mathematical standard profiles according to Eqn17 (blue line). A–C, eggs were purchased from Woodlands Farm, Canterbury and Staveleys Eggs Ltd, Coppull, UK.